

# A NEW MITRATE FROM THE UPPER ORDOVICIAN OF NORWAY, AND A NEW APPROACH TO SUBDIVIDING A PLESION

by A. J. CRASKE and R. P. S. JEFFERIES

**ABSTRACT.** This paper reconstructs, describes, and places systematically the mitrate *Barrandeocarpus norvegicus* sp. nov. from the Upper Ordovician (Hirnantian stage, Ashgill series) of Rambergøya in Oslo Fjord, Norway. This new species is the first mitrate described from Norway and a stem-group craniate in the plesion of *Mitrocystella*. To locate the species within its plesion in an objective manner, without using traditional categorial ranks, a number of new terms are proposed: a scion is a monophyletic group comprising a crown group and an adjacent crownward part of a stem group. A scion ought to be named after its basal plesion. Within a plesion, a first order apical group is a small monophylum (ideally a pair of sister species) further removed from the stem lineage than are any other species of the plesion, i.e. separated from the stem lineage by a greater number of phylogenetic segments (= species). The first order apical lineage is the direct line of descent leading from the stem lineage to the apical group. A first order paraplesion comprises all those members of a plesion which are equally closely related to the first order apical group. A first order parascion is a monophylum containing the first order apical group and one or more adjacent paraplesions, and should be named after its basal paraplesion. When a first order paraplesion contains several known species, it should be possible to recognize a second order apical group, a second order apical lineage, etc. and so on with still higher orders as the cladogram becomes more complex.

In these terms, *Barrandeocarpus norvegicus* is placed in the plesion of *Mitrocystella* in its own first order paraplesion. This is less apical than the parascion of *Ateleocystites guttenbergensis* (i.e. the Anomalocystitida in conventional terms) and more apical than the paraplesion of *Barrandeocarpus jaekeli* Ubaghs.

The locomotory cycle of *B. norvegicus*, crawling rearwards through the mud pulled by its tail, is reconstructed. The internal features of the head of *B. norvegicus* are similar to those of *Placocystites forbesianus* de Koninck in most respects, but show indications never seen before in mitrates, of the ventral surface of the hypophysis.

THE aims of this paper are to reconstruct, describe, and place systematically the mitrate *Barrandeocarpus norvegicus* sp. nov. from the latest Ordovician of the Oslo region, Norway, and to consider how a plesion should be subdivided.

The material on which this species is based was collected in July 1978 by Dr L. R. M. Cocks, of the Department of Palaeontology, British Museum (Natural History) and all of it is preserved at the BMNH. It was reconstructed, under the supervision of R. P. S. Jefferies, by A. J. Craske when working as a vacation student at the BMNH in the summer of 1985. The discussion of phylogenetic methodology in this paper, with particular reference to the placing of fossils within a plesion, is the work of R. P. S. Jefferies as also is the discussion of the systematic position of the species and of its locomotion. The account of the stratigraphy is by Dr L. R. M. Cocks.

## PHYLOGENETIC METHODOLOGY

The cladistic approach to fossils is a matter of dispute. In this section we shall first discuss the cladistic treatment of extant organisms and then argue that fossils, though they should be inserted into the same system as recent organisms, ought to be treated differently from these. Concerning recent organisms, we shall argue that paraphyletic groups are always regrettable, discuss why this is so, and advocate the abandonment of traditional categorial ranks (families, orders, etc.).

Concerning fossils, we assert that fossil groups must be defined, as well as recognized, on the basis of their features and that paraphyletic groups are necessary. We also distinguish between stem groups and stem lineages, discuss the division of stem groups into plesions, propose a standardized method for naming monophyletic groups that comprise a crown group and a crownward part of a stem group, and discuss how plesions may themselves be subdivided objectively.

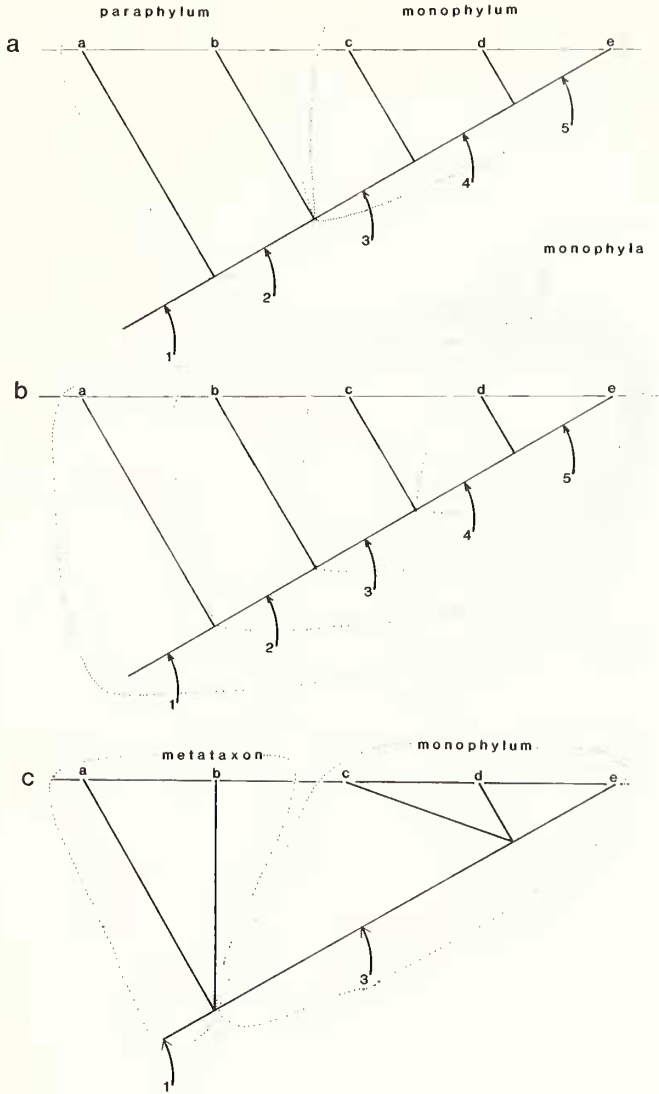
Our systematic viewpoint is fundamentally that of Hennig (1965, 1966, 1969, 1987) but has been influenced by Ax (1984, 1985, 1987), by Patterson and Rosen (1977), and by the penetrating philosophical essay of Griffiths (1976). We have also been affected by Fordham (1986) and Willmann (1985) who have discussed, in particular, the nature of fossil species and how such species should be treated when the fossil record is excellent.

Fossils differ from recent organisms, cladistically speaking, in two basic ways: 1, recent organisms are far better known than fossils, both as to percentage of species known and as to what is known, or knowable, about each species; and 2, recent organisms are accurately contemporaneous, whereas fossils differ in age. It is these two contrasts, but particularly the second, which imply that fossils cannot be systematized in exactly the same way as recent organisms. The fact that recent organisms are far better known than fossils makes them the starting point for systematic endeavours, though groupings based initially on recent organisms may be confirmed, modified, or sometimes even confuted, by information from fossils.

The exact contemporaneity of recent organisms, whereas fossils differ in age, has subtler implications. For, according to the biological species concept (Mayr 1963), a species is a population of interbreeding individuals separated from other such populations by mechanisms which prevent breeding. This implies, as Willmann (1985) has pointed out, that species owe their separate existence to barriers with respect to contemporaneous species, not with respect to species which existed in the past. This again implies, since an interspecific barrier to breeding normally works in two directions, that at a speciation event two new species arise, not one. In other words, a species is an undivided segment of the phylogenetic tree which originates at one speciation event and ceases, either by dissolution at the next speciation event which affects it, or else at extinction. If the present time can be taken as infinitesimal in duration, it follows that no extant species can be ancestral to any other extant species. This is the fundamental reason why a complete system of extant species will include nothing but monophyletic groups (= monophyla in Ax's convenient usage; 1984, p. 15) and single species. Nothing, however, prevents past species from being ancestral to other past species or to recent species. Indeed, every species must be descended from earlier species, and the fact that ancestor-descendant relationships are difficult to recognize does not lessen the certainty that they existed. It follows that any complete system containing extinct species must accommodate ancestors and must therefore include groups or species ancestral to non-members. Such groups are by definition paraphyletic (paraphyla of Ax 1984, p. 32). Some authors, such as Ax himself (1984, p. 209), have sought to systematize fossils without using paraphyla but all such attempts are doomed—the paraphyla are covertly there though not acknowledged.

Why ought the system of recent species to be constructed entirely of species and of monophyla? To illustrate the reason, text-fig. 1 shows the phylogenetic tree of a group of five extant species (a to e) and records the evolutionary origin of morphological features 1 to 5. It also shows two different ways, among many, of systematizing the five species—in text-fig. 1a the monophylum [c+d+e], characterized by feature 3, is distinguished from the paraphylum [a+b], characterized by feature 1 and by the primary lack of feature 3. In text-fig. 1b, on the other hand, the group [a+b+c+d+e], itself a monophylum characterized by autapomorphy 1, is recognized to contain four smaller monophyla, characterized respectively by features 2, 3, 4, and 5. Assuming that the phylogenetic relationships of the species in text-fig. 1 are completely known, then the system shown in text-fig. 1a implies an arbitrary decision. It implies, namely, that the origin of feature 3 is more important than that of 2, 4, or 5—important enough to have a group based upon it. The system shown in text-fig. 1b, on the other hand, is in no way arbitrary. It merely involves historical reconstruction, i.e. the placing of features 1 to 5 in their correct sequence of origin, on the basis of their observed distribution among recent organisms. In other words, features are commensurable

TEXT-FIG. 1. The non-objectivity of paraphyla in the systematization of extant organisms. *a*, the extant species a-e are placed in a monophylum [c-e] and a paraphylum [a-b], on the grounds that novelty 3 is 'more important than' novelties 2 or 4. *b*, an objective systematization using monophyla only. *c*, an objective systematization based on ignorance of the relationships of species a and b.

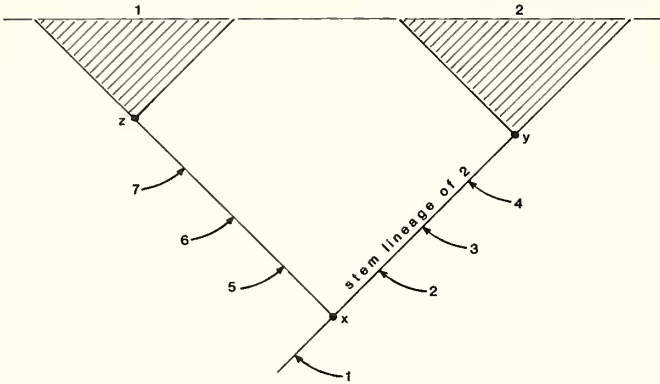


not in themselves, but only because they arose in the shared dimension of time. A system of monophyla for recent groups is based on reconstructing the origin of successive features in time and, as such, is an objective hypothesis which may be either right or wrong. Arbitrary and subjective decisions about the relative importance of features are simply not required for such a system.

Ignorance brings its own form of objectivity. If, in text-fig. 1a, the distributions of features 2, 4, and 5 were not known among recent organisms, it would then be legitimate, as a provisional measure, to divide the group [a + b + c + d + e] into the monophylum [c + d + e] and the paraphylum [a + b]. However, under these circumstances, [a + b] would not have been recognized as a paraphylum, for the best available cladogram would be as shown in text-fig. 1c. Gauthier (1986, p. 8) has referred to such groupings, doubtful whether monophyletic or paraphyletic, as metataxa.

The system of extant organisms is necessarily formed from inter-nested groups—of older more inclusive monophyla containing newer less inclusive monophyla. Each monophyletic group with





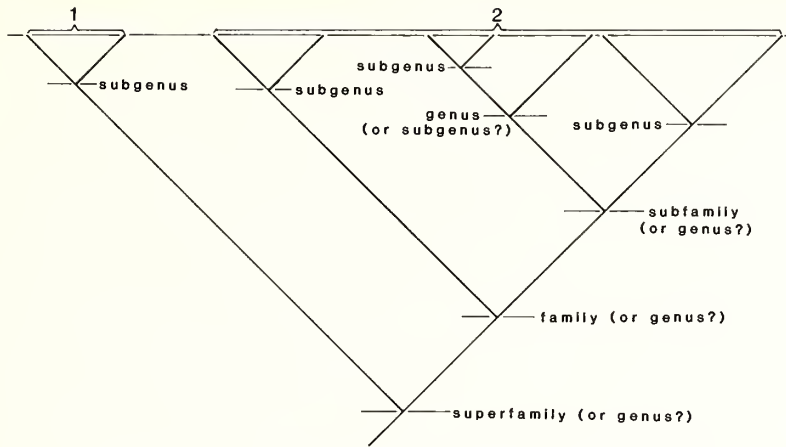
TEXT-FIG. 2. The extant sister groups 1 and 2 with their respective latest common stem species  $z$  and  $y$ , their shared latest common stem species  $x$  and autapomorphies (1-7) acquired in the respective stem lineages.

extant members will have one other extant monophylum, or one other extant species, more closely related to it than is any other among extant organisms. These were referred to by Hennig (1966, p. 139) as the sister group or sister species of the first-mentioned group, while Ax (1985, p. 16) has proposed the term adelphotaxon to cover both sister group and sister species. Every monophylum with extant members will have had in the past a latest common stem species. Every pair of adelphotaxa will itself form a monophylum with its own latest common stem species. A monophylum is recognized as such by possessing advanced features of its own—these are the autapomorphies of the monophylum and, as such, were not present in the latest common ancestor shared with the adelphotaxon. The line of descent exclusive to an extant monophyletic group and in which the autapomorphies of this group were acquired can be called the stem lineage (*Stamlinie* of Ax 1984, p. 6, though Ax's use of this term is somewhat ambiguous when applied to fossils, as discussed below). At a different level of analysis, the autapomorphies of a monophylum, by definition acquired in the stem lineage of this monophylum, are synapomorphies of the two largest adelphotaxa within the monophylum.

Text-fig. 2 makes this usage of the term 'stem lineage' more explicit. 1 and 2 are sister groups with extant members. All extant members of 2 share a latest common stem species  $y$  which is not shared with any other extant organism. Similarly, all extant members of 1 share exclusive descent from their latest common stem species  $z$ . And the two adelphotaxa together combine to form a larger monophyletic group, all members of which share an exclusive descent from their latest common stem species  $x$ . The stem lineage of 2 will run from  $x$  to  $y$  (though in our usage it excludes these two species populations). Features 2, 3, and 4, acquired in the stem lineage of group 2, will, if retained in  $y$ , be autapomorphies of group 2. Likewise features 5, 6, and 7, acquired in the stem lineage of group 1, between  $x$  and  $z$ , will be autapomorphies of group 1. And feature 1, acquired in the stem lineage of group [1 + 2], will be an autapomorphy of group [1 + 2] and a synapomorphy of groups 1 and 2.

Traditional categorial ranks cannot objectively be assigned to the groups in a phylogenetic system. The fundamental reason for this is that adelphotaxa will nearly always differ in the number of hierarchical levels which exist within them. Thus text-fig. 3 shows the phylogenetic trees of sister groups 1 and 2. These contain respectively two and seven species, while one hierarchical level exists in 1, as against four such levels in 2. If we attempt to apply to such a non-uniform 'truncated' hierarchy (Griffiths 1976) a traditional series of categorial ranks (subgenus, genus, subfamily, family, superfamily), should the group comprising [1 + 2] be regarded as a genus, since it contains two hierarchical levels with respect to the species in 1? Or should it be regarded as a superfamily, since it contains five hierarchical levels with respect to two of the species in 2? (There are similar, though smaller, discrepancies with respect to each nodal point within 2.) Any system which aims at assigning categorial rank to all the monophyla which exist will produce endless paradoxes of this sort. The only solution, explicitly advocated by Ax (1984, 1987), and adopted also, for example,





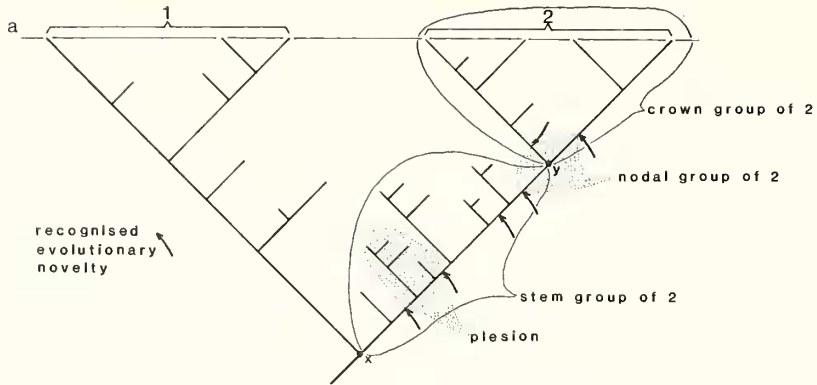
TEXT-FIG. 3. The arbitrariness of categorial rank (see text).

by Gauthier (1986, p. 8), is to abandon any formal system of categorial rank. This proposal departs uncomfortably from tradition, but also stops a well-spring of pointless quarrelling.

As concerns fossils, we have discussed the treatment of these elsewhere (Jefferies 1986, chapter 1; Jefferies *et al.* 1987) and we elaborate these earlier proposals here.

A fundamental difference between any group known only from extant organisms, on the one hand, and one known to include fossils, on the other, can also be illustrated from text-fig. 3. It concerns the distinction between definition and recognition. Thus group 2, for example, as to its recent members, can be *defined* exactly in terms of phylogeny—it comprises, namely, all extant descendants of the latest common stem species *y*. On the other hand, group 2 can be *recognized* as a monophyletic group because all its extant members have the autapomorphies 2, 3, and 4, the distribution of which among recent organisms is coextensive with group 2 (apart from secondary loss). Where fossils are concerned, however, the situation is more complicated. For features 2, 3, and 4 did not arise simultaneously but originated in that sequence in the stem lineage of group 2. There were forms more closely related to the extant members of 2 than to those of 1 (i.e. descended from *x* but not belonging to group 1) which primitively lacked features 2, 3, and 4; there were others which had 2 but primitively lacked 3 and 4; and others which had 2 and 3 but primitively lacked 4. (These forms would not all have been members of the stem lineage of 2, since some of them would have belonged to the side branches from that lineage.) It follows that groups containing fossils, unlike purely recent groups, must be defined, as well as recognized, in terms of their features, since the distribution of features reflects the phylogeny only inexactly.

As to the distinction between crown group and stem group, text-fig. 4 shows the phylogenetic trees for the sister groups 1 and 2 with extant representatives. Following Hennig (1969, 1983), there are two obvious delimitations of group 2, one narrow and one broad. The narrower delimits the group as the latest common stem species of 2, plus all descendants of that stem species. This delimitation defines the \*group of Hennig, which we call the crown group. The wider delimitation contains all those forms which are more closely related to the extant members of 2 (i.e. share a more recent common ancestor with them) than to the extant members of 1. This wider delimitation defines the total group of Hennig. By subtracting the crown group of 2 from the total group of 2, a paraphyletic assemblage remains called the stem group of 2. Through the stem group of 2 runs the stem lineage of 2 in our sense. This is the direct lineage of ancestors and descendants leading from *x* (the latest common ancestor of [1 + 2]) to *y* (the latest common ancestor of the extant members of 2), but excluding both *x* and *y*. In this lineage, the autapomorphies of 2 would have been acquired, and, in this respect, it corresponds to the stem lineage in the sense used by Ax



TEXT-FIG. 4. Stem group, crown group, nodal group, and plesion.

(1984, 1987) when discussing extant groups with no fossils. We should point out, however, that Ax, when discussing fossils, also uses the term 'stem lineage' or '*Stammlinie*' in a broader sense exactly equivalent to Hennig's 'stem group' (Ax 1984, 1987, chapter J). Here we explicitly exclude this broader sense of the term 'stem lineage'.

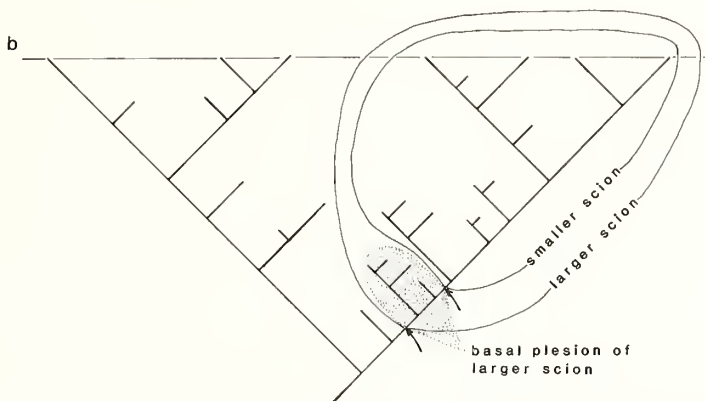
A plesion, for us, comprises all those members of a stem group which, so far as can be discerned, are equally closely related to the crown group. It therefore includes all those forms which possess, or have secondarily lost, one novelty acquired in the stem lineage, but primitively lack the next recognized novelty acquired in the stem lineage. For us, therefore, a plesion is, in principle, a paraphyletic grouping since it contains part of the stem lineage and this will have been ancestral to non-members of the plesion. This differs from the concept proposed by Patterson and Rosen (1977) and espoused by Ax (1984; 1987, chapter J) who all imply that plesions are, in principle, monophyletic and who thus have no place in their system for true members of a stem lineage.

Plesions, although in principle paraphyletic, can be defined and recognized objectively because they are made as small as possible. Thus, as soon as it can be shown that some members of a former plesion are more closely related to the crown group than others are, by demonstrating a previously unnoticed novelty in the contained part of the stem lineage, then the former plesion splits into two plesions, one more crownward than the other. In other words, the recognition of plesions is objective since it is based on reconstructing, so far as possible, the complete sequence of evolutionary novelties, as they actually happened in time, in the stem lineage.

A plesion can be delimited in terms of two monophyletic groups—the larger containing the smaller (text-fig. 5). Both groups would have the same extension among recent organisms, and would include the same crown group. Within the relevant stem group, however, they would differ in extension, in that the plesion in question would be included in the larger group but excluded from the smaller one. We propose that these partly fossil and partly extant monophyla should be called 'scions'. The name refers to the horticultural operation of grafting, in which a scion comprises all parts of a branch distal to the point cut through by the gardener. We propose that each scion should be named after the plesion included at its base. The reason for this proposal is that each monophylum has a unique latest common stem species, and could, ideally, be named after this stem species, if such could ever be identified (which it probably never can be). Naming a scion after its basal plesion is the best practicable approach to naming it after its latest common stem species. This procedure would standardize and simplify the naming of partly fossil monophyla.

The desirability of such standardization is exemplified by the recent work of Gauthier who has published an extremely thorough cladistic analysis of the origin of birds (1986; text-fig. 6 herein). In doing so, he implies a succession of nine plesions in the avian stem group. However, he does not describe the situation in terms of a stem group with plesions. Instead, he restricts the term

'Aves' to the crown group of the birds and sets up eight additional monophyla, each co-extensive with the Aves in the recent fauna, but differing in extent in the fossil fauna. To each of these eight additional monophyla he gives a name, not etymologically related to any particular member of the group and often new. For example, Gauthier's group Avialae differs from his group Ornithurae only by including the plesion of *Archaeopteryx*. We suggest that the Avialae could conveniently be referred to as the scion of *Archaeopteryx*, whereas the Ornithurae could perhaps be called the scion of *Hesperornis*. This would greatly reduce the burden on the reader's memory. The 'scion of *Archaeopteryx*' would not be the same as the 'monophylum of *Archaeopteryx*' since the latter expression would most naturally refer to a monophyletic group containing *Archaeopteryx* alone.



TEXT-FIG. 5. Two adjacent scions within a partly fossil, partly extant monophylum, and the name-giving basal plesion of the larger scion.

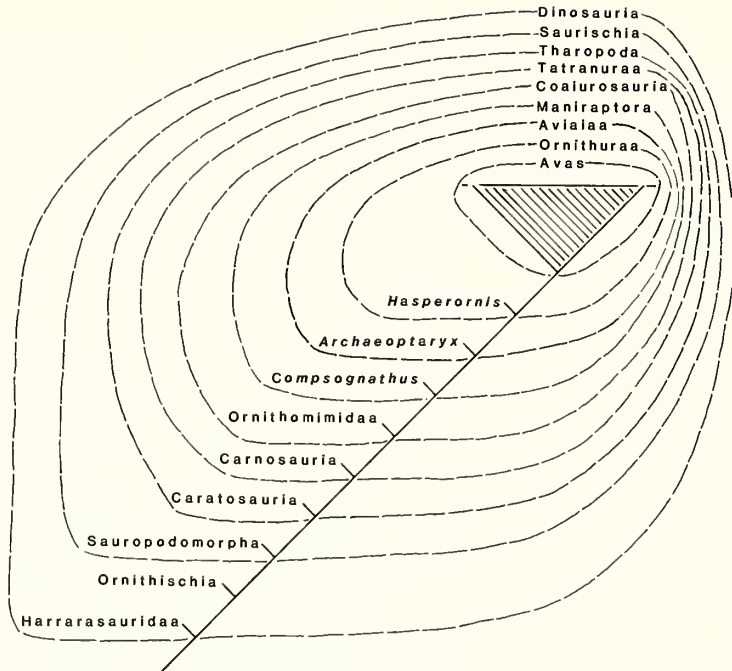
In naming a plesion, we ought not to use the name of any arbitrary member, nor even the name first given to the plesion in the literature. Rather it should be named after the known form most closely related to the stem lineage, and thus most closely related to the latest common stem species of the relevant scion. The name of a plesion, or of a scion, would therefore not be fixed by priority but would change as new forms, more closely related to the latest common stem species of the scion, were discovered. (Perhaps the choice of '*Hesperornis*' as the scion name for Gauthier's Ornithurae is for this reason unsuitable.)

We have proposed the term 'nodal group' (Jefferies *et al.* 1987, p. 432) for all those fossil members of an extant monophylum which possess all the autapomorphies of the crown group, but primarily lack any of the autapomorphies of any of the extant subgroups of the crown group. In this sense, the nodal group includes the latest common ancestor of the extant members of a group. We now extend the use of this term by speaking of the nodal group of a plesion to mean all those members of the plesion which, so far as known features are concerned, do not differ from the stem lineage. Whenever possible, a plesion should be named after a member of its nodal group.

Systematization within a plesion is the next problem to be considered and is especially relevant to the fossil described in this paper. We shall not use traditional categorical ranks since, as already pointed out, they cannot be assigned objectively. The problem, therefore, is to recognize and name monophyla and objective paraphyla within a plesion, without using traditional ranks and without creating names unnecessarily, i.e. the naming procedure for each included group should be related, in a standard way, to the contents of the group.

The real phylogenetic tree of a plesion will consist of part of the stem lineage of an extant monophyletic group, *plus* all side branches from that part of the stem lineage. If this real tree is

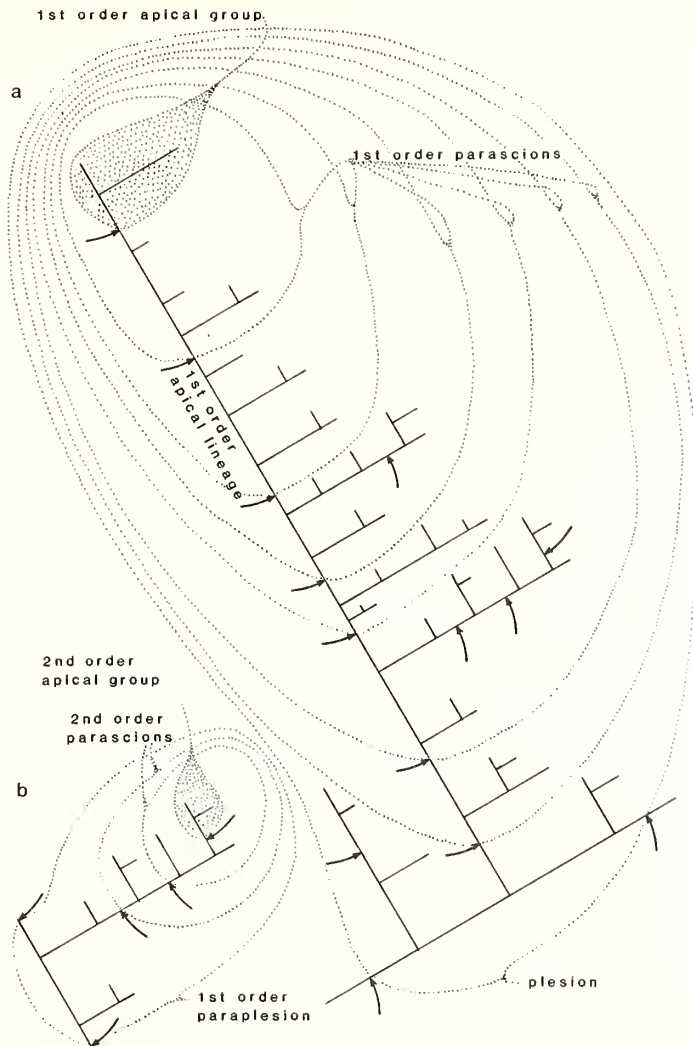




TEXT-FIG. 6. Monophyletic groups recognized in the evolution of birds.  
Modified after Gauthier (1986, fig. 8).

big and complicated, there will be a pair of sister species within it further removed from the stem lineage than any other such pair, i.e. separated from the stem lineage by a greater number of phylogenetic segments (= species). We propose to call this pair of species the real first order apical group of the plesion (first apex for short). The lineage leading from the stem lineage to the first apex can be called the first order apical lineage. All monophyla which include the first apex (text-fig. 7) can be called first order parascions (this name should suggest a scion cut off a side branch). There will have been successive evolutionary novelties in this apical lineage and, on the basis of these, the plesion can be divided into first order paraplesions (text-fig. 8), all members of any such paraplesion being, so far as discernible, equally closely related to the first apex. A first order paraplesion can equally be defined as comprising all those members of a plesion which are contained in one first order parascion, but not contained in the included next smaller recognizable first order parascion. So long as paraplesions are made as small as possible they are objective. This means that, if it can be shown that some members of a former paraplesion are more closely related to the relevant apex than other members, then that former paraplesion must be split into two paraplesions, one more apical than the other. If this is done, a paraplesion, though paraphyletic, is not arbitrary, depending, as it does, on the most complete possible reconstruction of evolutionary history.

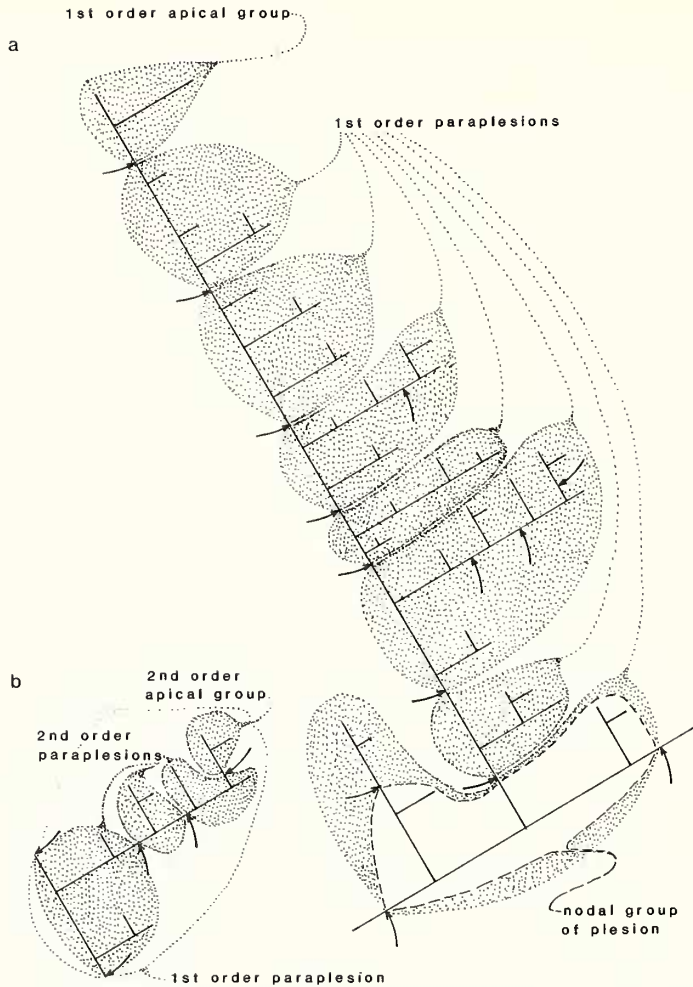
A first order paraplesion may itself contain several species and, if the branching is complicated, a pair of these species will be further removed from the first order apical lineage than is any other species of the paraplesion. This pair will constitute a second order apical group. Within the first order paraplesion it will therefore be possible to recognize second order paraplesions arranged in order of relationship to the second order apex. With any plesion of complicated and abundant branching there will be only one first order apex, but several second order apices. Similarly, a second order paraplesion may contain a third order apex and be divisible into third order paraplesions, and so on.



TEXT-FIG. 7. *a*, first order apical group and parascions in the real tree of a plesion. The curved arrows point to recognized evolutionary novelties. *b*, subdivision of a first order paraplesion. Compare text-figs. 8 and 9.

We suggest that parascions ought to be named after their least apical paraplesion, and that this ought to be named after that known included species which is most closely related to the relevant apical lineage. (As to what 'relevant' means here, in dividing a plesion into first order parascions and first order paraplesions, the apical lineage leading to the first order apical group is the relevant lineage.) This is analogous to the procedure suggested above for naming scions and is based on the same consideration—that such a procedure is the best practicable approximation to naming a monophylum after its latest common stem species.

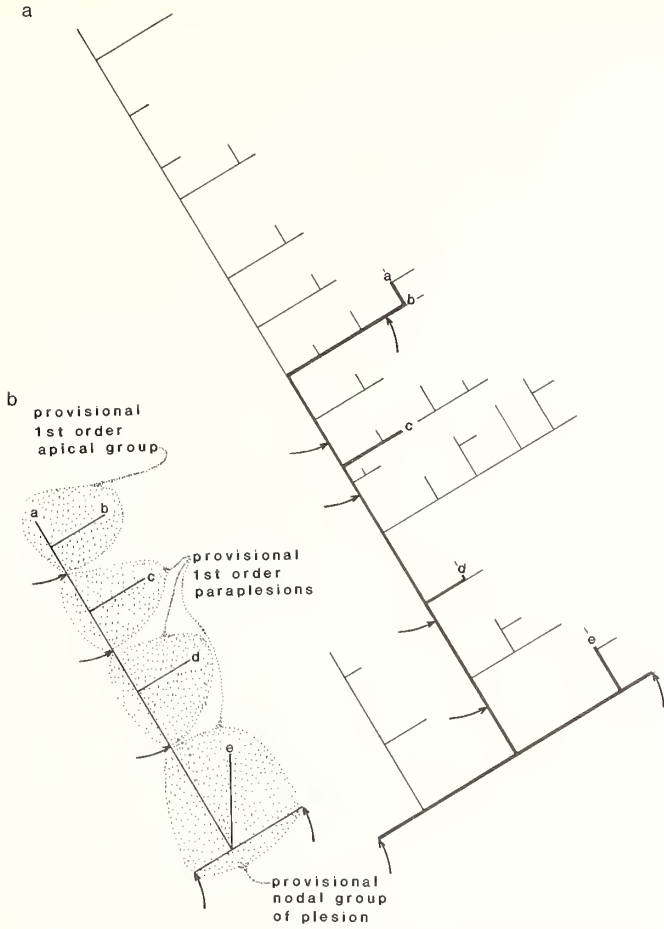
In palaeontological practice, we do not know the real phylogenetic tree of a plesion. However, if more than two species are known within a plesion, then it is likely that they can be placed on a cladogram, which we see as a reconstructed phylogeny formalized by placing at the ends of



TEXT-FIG. 8. *a*, first order apical group, paraplesions, and nodal group in the real tree of a plesion. *b*, subdivision of a first order paraplesion.

branches all the known forms considered. In this cladogram (text-fig. 9), a pair or a small number of species (probably sister species but possibly ancestors and descendants of each other) will be further from the stem lineage than the other known species are, i.e. separated from the stem lineage by a greater number of cladogram segments than any other known species is. This pair or small number of species will be the provisional first order apex of the plesion and the other species can be arranged in provisional paraplesions, each one of which will contain all species which, so far as discernible, are equally closely related to this first order apex. Thus, at any one stage of study, the known members of a plesion can objectively be arranged in a best possible approximation to the real phylogenetic tree. The best possible cladogram will change as new species are discovered and studied. It may be that the new species will lie distal to the first apex as originally set up, the members of which would thus become a first order paraplesion. Or it may be that numerous new members of what was originally a single paraplesion will be discovered, so that the recognized first apex shifts to that former paraplesion. Always, however, if a cladogram can be constructed, it will be possible to arrange the known members of a plesion in terms of apices and paraplesions, of





TEXT-FIG. 9. Relation between: *a*, a partly known plesion (in which the species *a-c* have been discovered); and *b*, its cladogram. The thick line in *a* represents the parts of the real tree which are represented in the cladogram.

first, second, or *n*th orders, as suggested here. As study proceeds, the arrangement will become steadily more complex and should converge on the topology of the real tree.

The naming of the constituent parascions and paraplesions of a plesion will change as the cladogram changes and will follow the rule already suggested—that a monophylum will be named after that known constituent species which is most closely related to the latest common stem species. Thus the names will change as the cladogram does but should, like the cladogram, converge on a stable condition corresponding to the true tree.

In describing and naming the parts of a river system, geographers use a procedure analogous to the one suggested here for systematization within a plesion. They consider, namely, the longest watercourse as being one river (first order apical lineage) and regard other watercourses flowing into it as different rivers (second order apical lineages). Traditional hierarchical ranks would suggest that the phylogenetic system is uniformly hierarchical like an army, with equal numbers of hierarchical levels in all its constituent groups of the same rank. In fact it is more like a drainage pattern, in which different rivers have different numbers of tributaries. Any sound approach to

describing the phylogenetic system must reflect the orderliness, and disorderliness, which evolution has produced in Nature. We hope that what we suggest here will contribute to that aim.

Thus the cladistic approach to fossil groups will, in one sense, be the same as to recent groups—whenever a monophylum can be recognized, it should be named and incorporated in the system. However, unlike recent groups, usable fossil groups must be defined, as well as recognized, by their features. Also, fossil studies strive towards a different end point from recent studies. For, with purely recent organisms, a system comprising nothing but monophyla and species is theoretically attainable, but with fossils, simply because some of them will have been ancestors, it is not.

#### SYSTEMATIC PALAEOLOGY

Superphylum: Deuterostomia Grobden 1908

Subsuperphylum: Dexiothetica Jefferies 1979

Phylum: Chordata Bateson 1886

Subphylum: Craniata Goodrich 1909

(Stem group of the Craniata)

Plesion of *Mitrocystella* Jefferies 1979

Paraplesion of *Barrandeocarpus norvegicus* herein

Genus *Barrandeocarpus* Ubaghs 1979

Species *Barrandeocarpus norvegicus* sp. nov.

#### *Systematic position*

This statement of phylogenetic position gives conventional categorial ranks (superphylum, etc.) for the higher ranking groups, but, as already discussed, such ranks have no objective meaning and will probably come to be abandoned (Ax 1984, 1987). The subphylum Craniata, as given here, is coextensive with the subphylum Vertebrata as used in Jefferies (1986). We now adopt Janvier's usage (1981) by which the term Vertebrata is restricted to the group [Petromyzonida + Gnathostomata] and Craniata is used for the wider group [Myxinoidea + Petromyzonida + Gnathostomata].

#### *Material, horizon, and locality*

All of the specimens described in this paper come from a single bedding plane 7.1 m above the top of the 'Brown Sandstone', which is a 1.5 m thick, heavily bioturbated sandstone marking the local base of the Langoyene Sandstone Formation. They were collected by Dr L. R. M. Cocks in July 1978. The locality is a natural beach outcrop at the south-western end of Rambergoya in the Oslo Fjord, Norway. The locality (text-fig. 10) is at grid reference NM 962394 and is 3.7 km south-south-east of Oslo Town Hall.

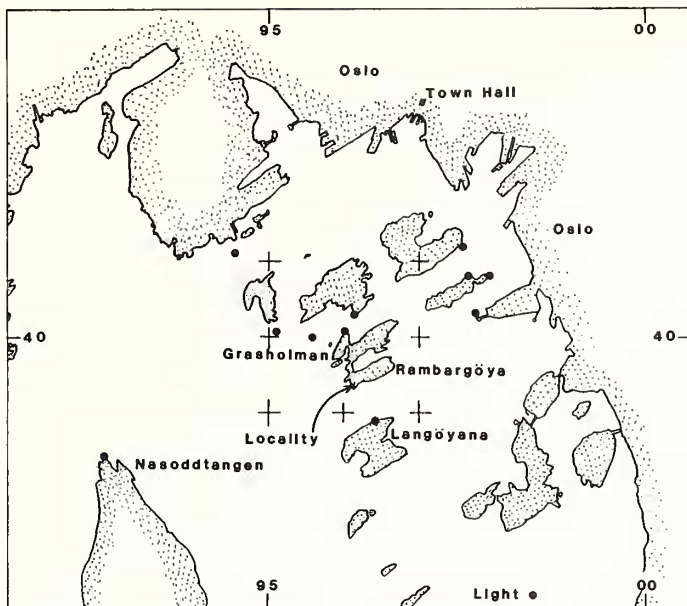
The bedding plane is not rich in fossils but the assemblage is dominated by the brachiopod *Eostropheodontia hirnantensis* (M'Coy), with *Barrandeocarpus norvegicus* the only other fossil collected in more than single specimens. The other fossils recorded are the brachiopod *Hirnantia?* sp., *Tentaculites* sp., a colonial bryozoan, and a crinoid ossicle.

Within the Brown Sandstone, however, and in the beds 2–3 m above it, there is a rich and diverse *Hirnantia* fauna of Hirnantian (latest Ashgill) age (Brenchley and Cocks 1982, p. 796, locality 197) and other Hirnantian faunas occur above the bedding plane with *Barrandeocarpus norvegicus*.

As to geographical conditions, in the late Ordovician the Oslo area was on the west of the palaeocontinent of Baltica and lay at a latitude of about 30° S. (Cocks and Fortey, 1982). During the Hirnantian stage there is much evidence of glacial deposits in and around the large Gondwana palaeocontinent which lay south of Baltica, but there were contemporary warm-water limestones in the equatorial North American palaeocontinent. It is likely, therefore, that *Barrandeocarpus norvegicus* lived and died in warm to temperate waters.

The material is all preserved in the British Museum (Natural History) and comprises remains of about fifty individuals. Some of it is part and counterpart (signified by *a* and *b* at the end of the registration number). Some of the slabs show more than one individual, in which case each individual was given a letter after the registration number. In the following list, an asterisk indicates a morphologically informative specimen.

The registration numbers are as follows: E29381a/a\*, b\*, c\*, d\* (holotype), e\*, f, l\*, m\*; E29381b/g\*, h\*, i, j, k\*, n\*; E29383a; E29384/a, b, c, d, e, f\*, h, i\*; E28385/a\*; E63163/a; E63164a/a\*; E63164b/a\*; E63165/a\*.



TEXT-FIG. 10. Map to show the locality for *Barrandeocarpus norvegicus* sp. nov. Traced from the Norwegian 1:50 000 sheets for Asker and Oslo. The numbers refer to the Norwegian national grid. The crosses, taken from the grid, are 1 km apart.

*b, c*; E63166/*a*\*; E63167/*a*\*; E63168/*b*; E63170/*a, b*; E63171/*a, b, c, d*\*, *e*; E63172/*a*; E63173/*a, b*; E63174/*a*\*; E63175/*b*; E63176/*b*/*a*\*; E63177/*a*\*; E63178/*a*.

The holotype (E29381/*a/d*) shows the most complete dorsal surface available.

Most specimens were preserved as calcite plates embedded in the rock, though the calcite has been removed by acid preparation. There is some crushing and dislocation, but the good articulation of many of the specimens suggests burial at, or immediately after, death.

#### Anatomical description

In this description, individual plates are labelled according to the system proposed in Jefferies and Prokop (1972) and expanded in Jefferies and Lewis (1978, figs. 29 and 30). Plates given the same letter or number in different species are thought to be homologous with each other. Four different notations are used simultaneously:

1. Some anterior and posterior marginal plates are given lower-case letters (*b, c, g, h, i, j, n*, and *p*) implying homology with plates in primitive mitrates and, in some cases, with the crownward cornute *Reticulocarpus hausi*.

2. Some marginal plates and all centrodorsal plates are given arabic numbers (1 to 12) implying homology with mitrates closely related to *Barrandeocarpus norvegicus*.

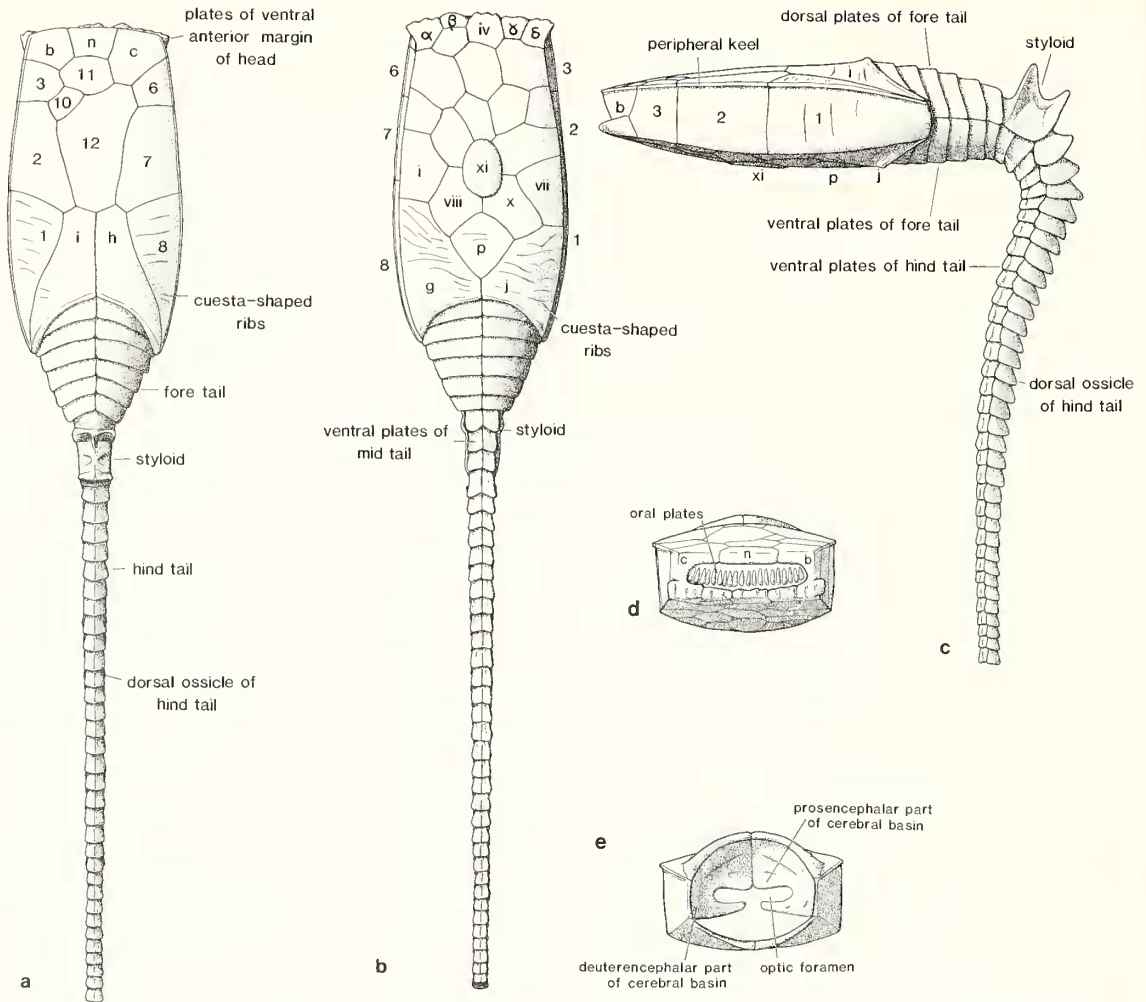
3. The ventral plates are, so far as possible, given lower case roman numerals, implying homology, in the first instance, with the specialized mitrate *Placocystites forbesianus*.

4. Four of the most anterior ventral plates are given Greek letters  $\alpha$  to  $\delta$ . These plates are constant in *B. norvegicus* but cannot certainly be homologized with plates in any other mitrate.

These different notations are complicated and difficult to remember but text-figs. 11*a-e* should clarify their meaning.

In general form, *Barrandeocarpus norvegicus* has a box-like head, with convex and probably





TEXT-FIG. 11. *Barrandeocarpus norvegicus* sp. nov. Reconstruction of external features: *a*, dorsal aspect; *b*, ventral; *c*, left lateral; *d*, anterior (the oral plates are purely reconstructural); *e*, posterior (tail omitted).

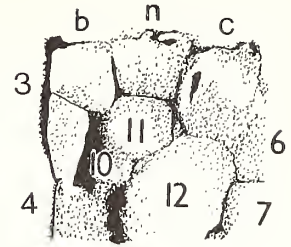
rigid dorsal and ventral surfaces. There is a projecting, but rounded, peripheral keel running along the lateral margins of the dorsal surface.

The fore tail is anteriorly almost as wide as the posterior part of the head, being almost circular at its proximal end. In dorsal aspect it narrows to where the styloid is situated. The hind tail is usually somewhat longer than the head, although in one specimen (Pl. 13, fig. 7) it is almost twice as long as the head.

*Dorsal surface of the head* (text-figs. 11*a* and 12). This is made up of fourteen plates, being three centrodorsals and eleven marginals.

The anterior margin of the head is framed by plates *b*, *n*, and *c*. These make a fairly straight edge, and constitute the upper lip of the mouth. There are three marginal plates along each side of the head, plates 1, 2, and (3 or 4) on the left and 8, 7, and (5 or 6) on the right. These six plates also form the lateral faces of the head.

TEXT-FIG. 12. *Barrandocarpus norvegicus* sp. nov. Explanatory diagram of Plate 12, fig. 2, showing plates in anterior part of dorsal skeleton.



The dorsal surface makes an angle of about  $90^\circ$ , or slightly less, with the lateral faces. Where they meet, the dorsal surface slightly overhangs the lateral faces, giving a keel along the edge (Pl. 12, figs. 1 and 5). Where the lateral and ventral faces meet there is no such keel, for the ventral plates abut against the marginals.

Plates i and h adjoin the posterior edge of the head. They do not help to form the posterior face.

There are three centrodorsal plates, one large one in a median position (plate 12) and two smaller ones anterior to and left of this (plates 11 and 10, respectively). Plate 11 can be seen plainly in several specimens (Pl. 12, fig. 2) but plate 10 is harder to trace. Its existence is shown by a triple junction on the median edge of plate 2 in one specimen (Pl. 12, fig. 2). The exact size and shape of plate 10 is uncertain. Plates 11 and 12 are almost bilaterally symmetrical but plate 10 lies to the left, being the only external sign of asymmetry in the dorsal skeleton.

In number and general position of plates the dorsal surface is identical both to *Ateleocystites guttenbergensis* as described by Kolata and Jollie (1982) and *Barrandocarpus jaekeli* as described by Ubahgs (1979). Differences are matters only of shape and proportion.

*Ventral surface of the head* (text-fig. 11*b*). This surface is again convex, but less so than the dorsal surface. It consists of about twenty-three plates which seem to have formed a rigid armour.

The plates of the posterior part of the ventral surface, forward to the transverse level of plate xi, are standardized between specimens, as also are the ventral plates adjacent to the mouth. Between these two regions, however, the plates vary considerably in number and position. All the plates of the ventral surface seem to be tessellate, giving a flush surface (except plate xi which protrudes somewhat). It is therefore likely that the entire ventral surface of the head was rigid (except, presumably, that it could warp slightly posteriorly, so that the atrial openings could gape). In having the anterior part of the ventral surface completely tessellate and completely rigid, *Barrandocarpus norvegicus* differs from *B. jaekeli*, where each plate of the anterior part of the ventral surface overlaps the posterior edges of its anterior neighbours.

The two largest plates in the ventral surface of *B. norvegicus* are plates g and j, which together form the posterior edge of the head in ventral aspect. Like plates i and h on the dorsal surface, they are more convex than the rest of the ventral surface, so as to accommodate the fore tail. There is a transverse ridge near the posterior edge of plates g and j (pl. 13, fig. 6). This, like a similar ridge in *Mitrocystites* and *Mitrocystella*, defines the anterior margin of the posterior surface. In *B. norvegicus* this surface is very small.

The other plates which appear to be standardized in the posterior part of the ventral surface are p, i (roman numeral), vii, viii, x, and xi.

Plate xi (the 'placocystid plate' of Caster 1952) is very peculiar. It is rounded rather than angular in outline (Pl. 12, fig. 11), and slightly more convex ventrally than the surrounding surface. Also, all other ventral plates have flat edges which meet at sutures perpendicular to the ventral surface, but the edges of plate xi slope dorsalwards toward the centre of the plate, making it a truncated cone with the internal surface smaller in area than the external surface. The edges of the adjoining plates (viii, x, and three unnamed, irregular more anterior plates) are sloped to receive plate xi.

In related species plate xi is likewise markedly different from the other ventral plates (Jefferies 1984). In addition to the peculiarities already mentioned in *B. norvegicus* (accentuated ventral convexity, non-angular outline, and truncated conical shape), there are two other distinctions, as follows:

1. It lacks ornament when its neighbours are ribbed, as seen in *Atelecystites guttenbergensis* and *B. jaekeli*; this distinction seldom holds in *B. norvegicus* for, though plate xi is always ribless, the neighbouring plates are usually ribless also.

2. It is very variable in size and does not enlarge as the head grows (as shown by an ontogenetic series in *Placocystites forbesianus* (Jefferies 1984))—these distinctions may or may not apply to *B. norvegicus*, since the known specimens do not vary enough in size to give a plausible ontogenetic series.

The anterior edge of the ventral skeleton of *B. norvegicus* is, in all observed cases (Pl. 12, fig. 8), made up of five plates arranged in bilateral symmetry. In text-fig. 11*b* these have been labelled  $\alpha$ ,  $\beta$ , iv,  $\gamma$  and  $\delta$ . These plates have a fairly prominent anterior edge while the parts nearest the mouth are bent upward to form the lowest portion of the anterior surface of the head. By comparison with *A. guttenbergensis* (which, as shown below, was more apical in the plesion) and with *B. jaekeli* (which was less apical in the plesion), there were probably spike-like oral plates in the lower lip of *B. norvegicus*, but no traces of these were observed. Text-fig. 11*d* shows a reconstruction of the anterior face of the head, including such oral plates.

The five plates which form the anterior edge of the ventral skeleton carry a series of external projections on this edge. These projections are particularly prominent on the leftmost and rightmost plates.

The ventral surface of *B. norvegicus* is in most ways similar in its constituent plates to those of *B. jaekeli* and *A. guttenbergensis*. However, there is a morphological series in which the plates become increasingly standardized and the surface increasingly rigid. This series passes from *B. jaekeli* (flexible anteriorly and the least standardized in its plating) to *B. norvegicus* (rigid throughout, standardized posteriorly and at the anterior margin) to *A. guttenbergensis* (rigid throughout and standardized throughout).

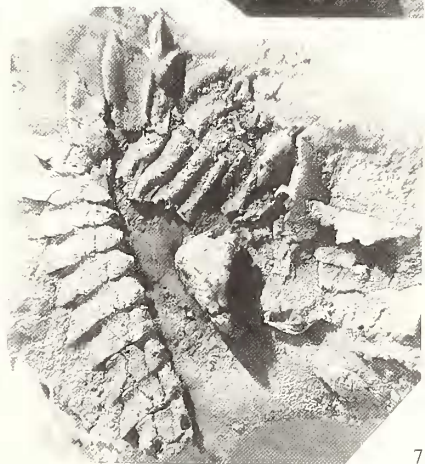
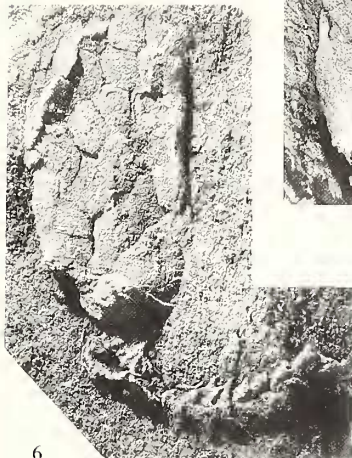
A few cuesta-shaped ribs exist on the head plates of *B. norvegicus*. On the ventral surface they are always found on plates g, p, and j and sometimes on plates immediately anterior to these except for plate xi which, as in related forms, is never ornamented (Pl. 12, figs. 6 and 11). On the dorsal surface ribs are found on plates l, i, h, and 8 (Pl. 12, fig. 5) though there is always a medial

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#### EXPLANATION OF PLATE 12

Figs. 1–11. *Barrandeocarpus norvegicus*. Latex casts of specimens. 1, E29381*a/d*;  $\times 5$ . Dorsal surface of holotype. Most of the plates of the dorsal surface can be seen except 10. Note peripheral keel, cuesta-shaped ribs, and the form of i and h near the tail insertion. 2, E29381*a/c, d*;  $\times 5$ . Anterior part of dorsal surface. Note peripheral keel on plates 7 and 8. Plates 11 and 12 are visible and the evidence for the position of plate 10 shows as an obtuse point (triple junction) on plate 2 (arrowed). Compare text-fig. 12. 3, E63162*b*;  $\times 5$ . Latex. Left side of head with peripheral keel, fore-tail plates and cerebral basin. 4, E29381*a/m*;  $\times 5$ . Dorsal ossicles and ventral plates of hind tail in right lateral aspect. 5, E29381*a/c, d*;  $\times 5$ . Specimen *d* (the holotype) overlies *c*, the posterior dorsal surface of which is seen at the top of the figure. Specimen *d* exposes the dorsal surface and clearly shows i, h, l, 8, and 12. The peripheral keel can be seen on 8, together with cuesta-shaped ribs on 1 and 8. Anteriorly the dorsal surface is missing, allowing the interior surfaces of a, b, iv, e, and d to be seen. 6, E29381*b*;  $\times 5$ . Ventral surface of head and ventral aspect of styloid and hind tail. Note cuesta-shaped ribs on g, p, and j. 7, E29381*b/g*;  $\times 5$ . Fore, mid, and hind tail. 8, E29384*i*;  $\times 10$ . Anterior part of the ventral surface of the head. Note the most anterior five plates  $\alpha$ ,  $\beta$ , iv,  $\gamma$ , and  $\delta$  and the irregular plates behind them. 9, E29385*a*;  $\times 2.5$ . Complete animal in left aspect to show common observed posture. 10, E63161*h*;  $\times 7.5$ . Dorsal aspect of styloid. Note sharp ridge connecting the two transversely elongate blades. 11, E63161*h*;  $\times 10$ . Latex of posterior part of ventral surface of head. Note plate xi and cuesta-shaped ribs on plates viii, x, g, p, and j.





ribless strip. Plates 1 and 8 also carry ribs on their lateral faces. Thus, cuesta-shaped ribs are confined to the posterior third of the head but are there found ventrally, dorsally (except for the medial strip), and laterally.

Comparing the ribbing with other species the dorsal distribution of ribs is similar to that of *B. jaekeli*. However, on the ventral surface *B. norvegicus* has far fewer ribs than *B. jaekeli*, in which the posterior two-thirds is ribbed. *A. guttenbergensis* has more ribs than *B. norvegicus* on both surfaces, but fewer than *B. jaekeli*. The relative sparsity of ribs on *B. norvegicus* may be due, at least in part, to the small size of the animal. For the head measures about 10 mm in length on average (e.g. specimen E63176/b in Pl. 13, fig. 6), whereas *A. guttenbergensis* is somewhat larger (some individuals reach a head length of 25 mm according to Kolata and Jollie 1982) and *B. jaekeli* is much larger (about 30 mm head length). This can be related to the situation in the ontogenetic series of *P. forbesianus* where Jefferies (1984) noted that large specimens have many ribs while small ones (presumed juveniles) have far fewer. In these juveniles the ribs were located as in *B. norvegicus*—on the posterior right and left areas of the dorsal surface and the posterior part of the ventral and lateral surfaces.

*The tail.* As in all known mitrates, the tail has three distinct regions—the fore, mid, and hind tail.

The skeleton of the fore tail is made up of six rings (Pl. 13, fig. 8), each consisting of four plates (right and left dorso- and ventrolaterals) sutured together to make the ring inflexible. Each ring overlaps the ring posterior to it. The sutures in each ring are in the dorsal and ventral mid-lines and left and right. Plate 12, fig. 7 shows the plates separated at these sutures.

The fore tail is almost circular in section where it joins the head and so makes up almost the whole posterior aspect of the head. It narrows rearwards to about two-fifths of its anterior width and the depth reduces only to about two-thirds of the anterior depth. Thus the distal end of the fore tail is elliptical and laterally compressed in section.

The skeleton of the mid tail consists of the styloid and associated plates. As in all known mitrates except the stem-group acraniate *Lagynocystis* (Jefferies 1973, 1986), the styloid seems to represent two ossicles of the hind tail fused together and otherwise modified. It articulates in *B. norvegicus* with two pairs of ventral plates, again as in all known mitrates except *Lagynocystis*.

The styloid (text-fig. 13) is complex in structure, with two transversely elongate blades dorsally, connected by a median ridge (Pl. 12, fig. 10). The anterior blade is the taller of the two and is slightly wider than the proximal part of the hind tail. Anterior to this blade, the styloid decreases in height and is overlapped by the posterior part of the dorsal region of the fore tail. The blade itself is concave on its posterior face which is divided into two by the median ridge. This ridge is

#### EXPLANATION OF PLATE 13

Figs. 1–9. *Barrandocarpus norvegicus* sp. nov. Latex casts and natural moulds. 1, E63166;  $\times 10$ . Ventral aspect of posterior part of natural internal mould. Note the posterior coelom, bounded anteriorly by a transverse fissure in the rock, and the likely position of the hypophysis, showing as a swelling posteriorly in the mid-line. 2, E63161a;  $\times 10$ . Ventral aspect of natural internal mould. Note twin buttons on plate xi and the two large buttons flanking this plate. Compare text-fig. 17. 3, E63177;  $\times 10$ . Natural mould of cerebral basin, imitating the brain. Compare text-fig. 18. 4, E63165;  $\times 10$ . Ventral aspect of a contorted natural internal mould of the head (same specimen as fig. 5). The transverse groove about one-quarter of the length forward from the posterior end is the anterior boundary of the posterior coelom. 5, E63165;  $\times 10$ . Dorsal aspect of contorted internal mould (same specimen as fig. 4). Compare text-fig. 16. 6, E63176b/a;  $\times 10$ . Plates of the ventral surface preserved as calcite. Note plate xi, rounded in outline and slightly protruding from the surrounding plates. Cuesta-shaped ribs on g, p, and j. Styloid shows in ventral aspect. 7, E29381a/b;  $\times 5$ . Latex showing twenty-seven segments of hind tail, lit from beneath. 8, E29381b/n;  $\times 5$ . Fairly complete left lateral aspect of head and part of tail, lit from beneath. Note fore tail and styloid and plate d, showing its junction with plates b and (3 or 4) and with the rest of the ventral surface. The upside-down individual is specimen k. 9, E63161/e;  $\times 5$ . Posterior part of natural internal mould of head, in dorsal aspect. Compare text-fig. 15.





1



2



3



4



6



7



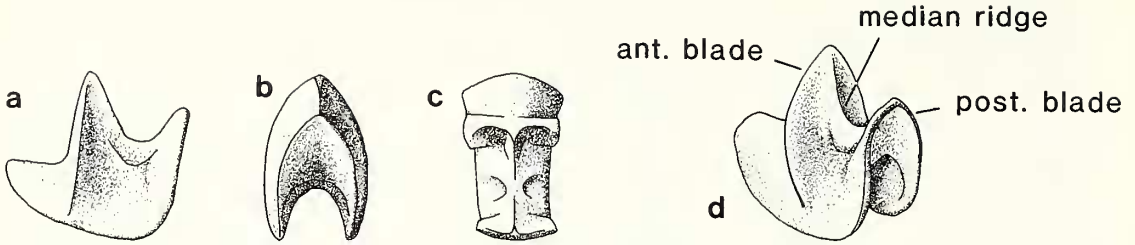
5



9



8



TEXT-FIG. 13. *Barrandeoecarpus norvegicus* sp. nov. The styloid: *a*, left lateral aspect; *b*, posterior; *c*, dorsal; *d*, left posterodorsal.

sharp-edged and continues rearward into the anterior face of the posterior blade of the styloid which is also concave rearward.

The successive segments of the hind tail do not much decrease distally in width but lessen in height (Pl. 12, fig. 7). As in all other mitrates, the skeleton of each segment of the hind tail consists of three calcite elements—two ventral plates and one dorsal ossicle. The ventral plates are joined ventrally in the mid-line, while the dorsal ossicle overlaps slightly the dorsal edges of these plates. The posterior part of each segment of the hind tail overlaps the anterior edge of the segment behind it.

Each pair of ventral hind-tail plates has a flattened ventral surface, from which the left and right sides rise almost vertically. In the larger specimens there is a distinct bulge at the bottom of these vertical sides. There also seems to be a slight ridge or lip on the anterior edge of the ventral plates, but normally this is hidden by the plate next anterior overlapping this area (Pl. 13, fig. 7).

Most specimens that retain the tail have up to twenty segments in the hind tail. No specialized terminal segment has been found. As with all other described mitrates, the tails seem to be broken off at their distal ends. The structure of the tail would allow a little flexion from side to side in the fore tail. Considerable dorsoventral flexion would be possible throughout the length of the tail.

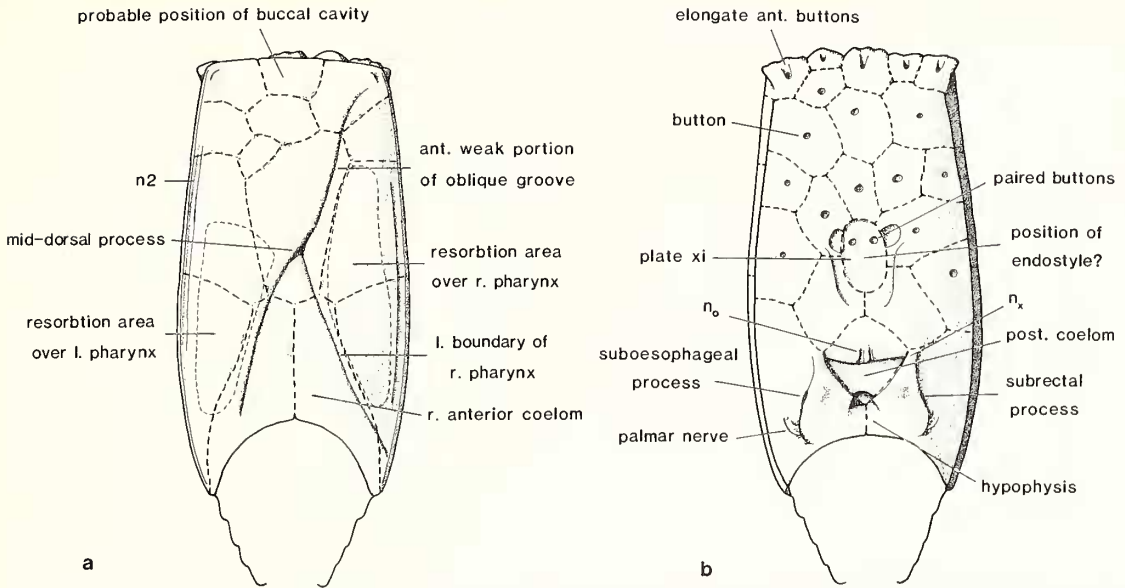
The fore and hind tail are similar to those in *B. jaekeli* and *A. guttenbergensis*. The styloid differs, however, in that neither of the other two species seems to have the transversely elongate blades of *B. norvegicus* and, in particular, the posterior blades in *B. jaekeli* and *A. guttenbergensis* are longitudinally, not transversely, elongate. In these respects, the styloids of *B. jaekeli* and *A. guttenbergensis* are probably primitive, since they are more like the hind-tail ossicles of these same species and also more like the styloids of *Mitrocystites*, *Mitrocystella* and *Placocystites*.

*Introduction to internal anatomy of the head.* A detailed description of the internal anatomy of the mitrate head is given in Jefferies and Lewis (1978) and Jefferies (1986). In these works it is argued that some mitrates are stem-group craniates (there called stem-group vertebrates) and that all mitrates fed by means of a mucous filter inside the pharynx, as seen today in tunicates, acraniates, and the ammocoete larvae of lampreys. Evidence is also given that the brain and cranial nervous system were fundamentally similar to those of vertebrates today. Inside the tail, a dorsal nerve cord, spinal ganglia, and a notochord are deduced to have existed.

There are two complementary ways of deducing internal features—examination of: 1, the internal surfaces of plates (or of latex casts of natural moulds of plates); and 2, of natural moulds. The natural moulds are helpful in reconstruction because they represent positives in rock of the soft parts. Unfortunately, the natural moulds available for *B. norvegicus* are imperfect.

*Dorsal features of the natural mould* (text-fig. 14*a*). Incomplete dorsal surfaces of the natural mould are seen in two specimens (Pl. 13, figs. 5 and 9), while much of the internal surface of the calcite plates can be seen in others. There are also other specimens showing smaller areas. Text-fig. 14*a* is a reconstruction of an idealized natural mould in dorsal aspect.

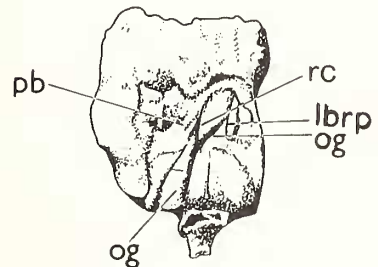




TEXT-FIG. 14. *Barrandeocarpus norvegicus* sp. nov. Reconstructed internal mould of the head, representing the soft parts. *a*, dorsal aspect. *b*, ventral aspect.

The most obvious feature of the dorsal surface of the mould is the oblique groove which runs across the head from anterior right to posterior left (Pl. 13, fig. 9; text-fig. 15). As argued by Jefferies (1986, chapter 8), this groove separated the fields of the right and left anterior coeloms. A second, weaker groove runs from approximately the centre of the oblique groove towards the right posterior corner of the head. This weaker groove divides the right field into two parts and represents the left boundary of the right pharynx, i.e. the limit between the right pharynx and the cavity of the right anterior coelom. No signs of the posterior boundary of the buccal cavity could be seen, although such a cavity presumably existed. Peripheral ridges (Pl. 13, fig. 5; text-fig. 16) run along the lateral edges of the natural mould and represent nerves  $n_2$  (in vertebrate terms the maxillary branches of the trigeminal nerve). The brain is discussed below. As in *P. forbesianus* and *A. guttenbergensis*, flat raised areas are visible on the dorsal surface of the natural mould over the right and left pharynges. Since these areas run without break across plate junctions, they probably represent resorbtion of the internal layers of the skeleton during life, and replacement of the calcite by soft connective tissue.

*Ventral features of the natural mould* (text-fig. 14*b*). The ventral surface of the natural mould is more complex than the dorsal surface but, fortunately, is shown by more specimens.

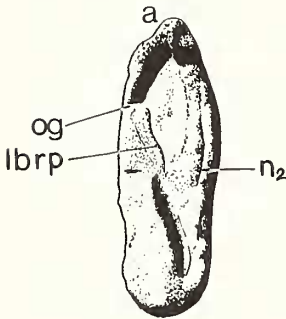


TEXT-FIG. 15. *Barrandeocarpus norvegicus* sp. nov. Explanatory diagram of Plate 13, fig. 9. lbrp = left boundary of right pharynx; og = oblique groove; pb = plate boundary; rc = resorbtion cliff in region of left pharynx.

Most plates in the anterior part of the ventral surface of the head, as far rearward as plates i, vii, and xi, carry a protrusion on the internal surface evident on the internal mould as a pit (Pl. 13, figs. 2 and 4). These 'buttons' were simple disc-shaped columns of calcite, usually at the centre of the plate and concave-sided and concave- or convex-topped. They represent the inner layer of calcite for this region of the skeleton.

Some plates, however, have buttons differing from the usual structure. Thus, the buttons of the plates at the anterior edge of the ventral skeleton ( $\alpha$ ,  $\beta$ , vi,  $\gamma$ ,  $\delta$ ) have ridges running forward from the plate centres, evident as grooves in the natural mould. Also, plate xi seems to be unique in having two normal-sized buttons, instead of one (Pl. 13, fig. 2). These buttons are paired and lie forward of the centre of the plate. Possibly the endostyle ran between these two buttons.

There are two other areas where inner-layer calcite has formed button-like depressions in the natural mould, these being on the plates anterior to plates viii and x, adjoining plate xi. Each of these plates has two buttons, that nearer the median plane of the animal being much larger than the other and located near the boundary with plate xi. The smaller button is central on these plates as is normal (Pl. 13, fig. 2; text-fig. 17). Sometimes there is a faint ridge of calcite running rearward from the larger buttons on to plates viii and x, approximately along the edge of plate xi.

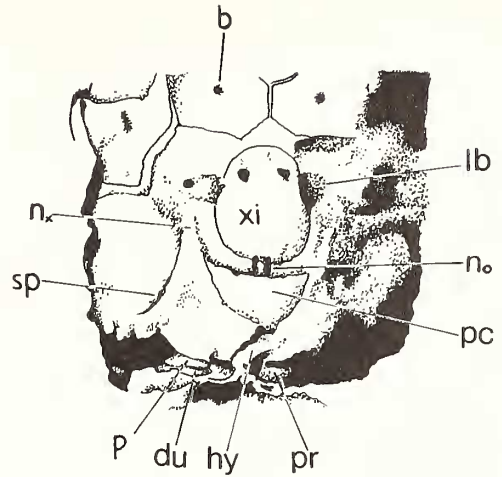


TEXT-FIG. 16. *Barraudeocarpus norvegicus* sp. nov. Explanatory diagram of Plate 13, fig. 5. Dorsal aspect of distorted internal mould of head. lbrp = left boundary of right pharynx; og = oblique groove;  $n_2$  = right nerve  $n_2$ .

The posterior part of the ventral surface of the natural mould has a fairly complex structure, and is best described by reference to text-figs. 14*b* and 17 (the latter being a diagram of Pl. 13, fig. 2). The posterior coelom shows itself on the natural mould as an approximately semicircular area at the posterior end of the head. In the natural mould this region is delimited by a transverse fissure anterior to it and by a pair of fissures anterolateral to it on left and right. As in *Placocystites*, the nerves  $n_x$  would have emerged left and right of the transverse anterior fissure (Jefferies and Lewis 1978, fig. 25; Jefferies 1986, fig. 8.25). The anterolateral fissures would represent walls of calcite in the skeleton—by comparison with *Placocystites*, these walls would perhaps have supported a suboesophageal process on the right and a subrectal process on the left (Jefferies 1986, chapter 8). To right and left of them the palmar nerves would have passed out of the posterior coelom. In the mid-line of the posterior coelom, at the posterior end of the head, there is a slight protuberance in the natural mould. This protuberance underlies the mid-line of the brain, being situated just beneath the place where left and right hypocerebral skeletal processes end beneath the brain without meeting. This position suggests that the protuberance may represent the position of the hypophysis (in vertebrate terms) or of the neural gland (in tunicate terms).

Channels for nerves  $n_o$  are clearly visible as grooves in the natural mould leading from the posterior coelom towards plate xi. (Jefferies and Lewis (1978) and Jefferies (1986) argued that the nerves  $n_o$  supplied the endostyle.) In the specimen shown in Pl. 13, fig. 2, these grooves reach plate xi. However, the positions of the plates of this specimen, together with its size, suggest that it is a juvenile. In a mature specimen, there would be a larger gap between the posterior coelom and plate xi, as indicated in text-fig. 14*b*.

TEXT-FIG. 17. *Barrandeocarpus norvegicus* sp. nov. Explanatory diagram of Plate 13, fig. 2; ventral aspect of natural internal mould of head. b = button (natural cast of inner layer calcite at centre of plate); du = deuterecephalon; hy = hypophysis; lb = large button just lateral to plate xi;  $n_o$  = nerve  $n_o$ ;  $n_x$  = nerve  $n_x$ ; pc = posterior coelom; pr = prosencephalon; sp = suboesophageal process; xi = plate xi, with paired buttons.

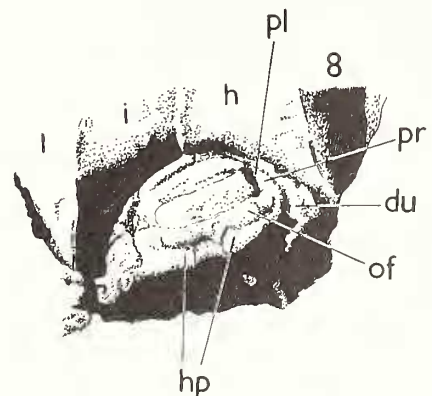


*The cerebral basin, brain, and tail.* Four plates of the head are in contact with the tail, g, j, i, and h. Anterior to the tail, plates h and i form a basin which is deduced to have contained the brain. The front wall of this basin would have separated the brain from the general cavity of the head. The basin is divided into a central, more anterior portion, in life containing the prosencephalon, and a more peripheral shallower portion corresponding to the deuterecephalon. Anteroventrally (text-fig. 18; Pl. 13, fig. 3), the prosencephalar portion of the basin is penetrated by the transversely elongate optic foramen, beneath which are the paired hypocerebral processes which almost meet each other in the mid-line. The cerebral basin, and therefore the brain, is very similar to that seen in other mitrates such as *Mitrocystella* and *Placocystites* (Jefferies 1986, chapter 8).

No internal details of the tail were observable, except that no dorsal longitudinal canal existed in the styloid or in the hind tail. In this respect, *B. norvegicus* differed from *Mitrocystella* and *Mitrocystites* but resembled *Placocystites* and perhaps all other members of the Anomalocystitida.

#### LOCOMOTION IN *BARRANDEOCARPUS NORVEGICUS*

Text-fig. 19 reconstructs the locomotory cycle of *B. norvegicus*, as it crawled rearwards through the top layer of mud in the sea bed. The reconstruction is based on an adjustable model in which



TEXT-FIG. 18. *Barrandeocarpus norvegicus* sp. nov. Explanatory diagram of Plate 13, fig. 3. Natural mould of the cerebral cavity representing the brain in anteroventral aspect. l, i, h, 8 = dorsal plates of the head; du = deuterecephalon; hp = hypocerebral processes; of = optic foramen; pl = plate of fore tail pushed in to form a pit in the rock; pr = prosencephalon.

a flexible rule was used to imitate the notochord as described for some other mitrates in Jefferies (1984) and for the cornute *Protocystites menevensis* in Jefferies *et al.* (1987). The use of a flexible rule is appropriate since, like a notochord, it can bend but not shorten or lengthen. The pictures ignore any yaw in locomotion. Unlike some other mitrates, *B. norvegicus* had an elongate head, so yaw was, indeed, probably small. In this respect, therefore, text-fig. 19 is probably not misleading. Obviously the graphical reconstruction can be no more than suggestive, but it brings the difficulties and mechanical requirements into focus.

A rearwards direction of movement in *B. norvegicus*, probably like that of all other calcichordates, is indicated by the cuesta-shaped ribs on the head, which, as in all other mitrates that possess them, consistently have the steeper slope anterior. They can be compared with the cuesta-shaped ribs of recent crabs and bivalves (Jefferies 1986, p. 248) which, by gripping sandy or silty sediment, serve to reduce movement in the wrong direction during the return stroke of the locomotory cycle. The belief that the tail moved mainly ventral to the head is based partly on the observed position of the tail in specimens of *B. norvegicus* (Pl. 12, figs. 4, 6, 7, 10) and partly on the fact that the same posture is deduced to hold for all other mitrates (Jefferies 1984). This deduction is particularly well founded for *Placocystites* (Jefferies 1986, fig. 8.18), in which plated, overlapping, dorsal folds in the fore tail would stretch and disappear when the tail flexed ventrally in locomotion. The view that *B. norvegicus* moved just beneath the surface of the sea bed is based on the fact that the right and left parts of the dorsal surface are ribbed but the median part ribless. This suggests that sediment was gripped by the ribs as it passed, in some thickness, at right and left over the dorsal surface but medially, where the head stood higher than the right and left portions, the dorsal surface was either unburied, or too thinly buried for the mud to be grippable. Ribs are similarly present at right and left of the dorsal surface, but absent medially, in all members of the parascion of *A. guttenbergensis* (the traditional group Anomalocystitida) and in *B. jaekeli*, and the same functional explanation probably holds for this pattern in all these forms. On the ventral surface in *B. norvegicus*, *B. jaekeli*, *Mitrocystella incipiens*, and Anomalocystitida with elongate heads, the transverse ribbing is not interrupted near the mid-line—presumably because the ventral surface was everywhere in contact with grippable sediment beneath.

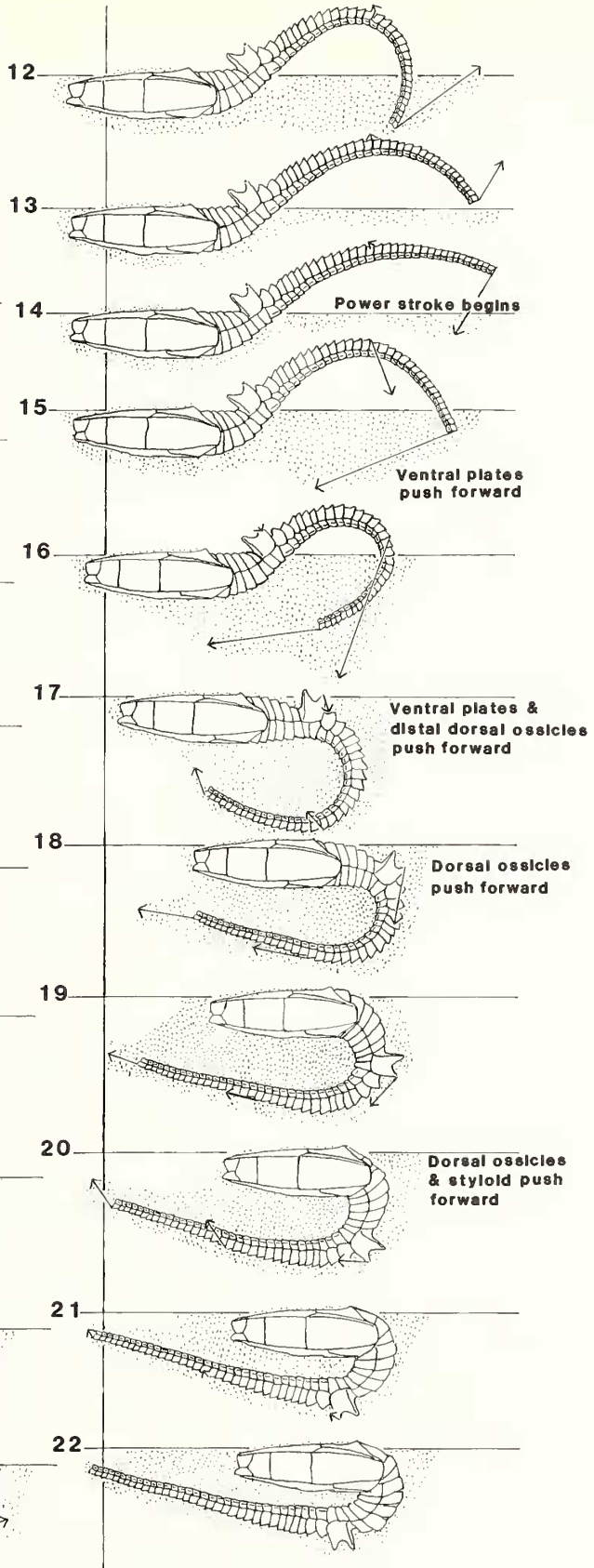
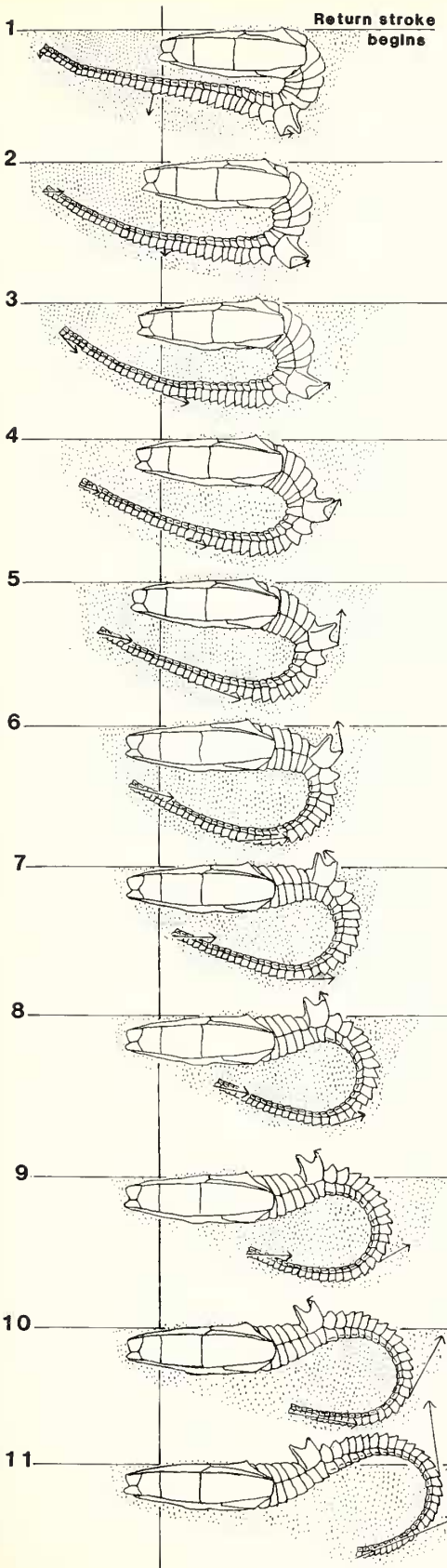
As against this, there are some mitrates which have ventral ribs at right and left but a central ribless area ventrally. This is true, for example, of *Placocystites* and of *Mitrocystites* (Jefferies 1984). The dorsal and ventral patterns of such forms are thus, at first glance, similar (though in *Placocystites* the ribbing on the dorsal surface ends abruptly in a median direction, whereas the ribbing on the ventral surface breaks up and fades out gradually towards the centre). The functional reasons are probably not the same, however. For the forms with the central, ventral ribless patch have relatively broad heads and this suggests that they yawed strongly in locomotion, alternately pivoting about right and left sets of ventral ribs. If so, they would have no use for ventral ribs placed centrally, for these could never be used as a pivot. Forms like *B. norvegicus*, in which the head is elongate, most likely did not yaw, and have medianly placed ventral ribs in consequence (Pl. 12, figs. 6 and 11; Pl. 13, fig. 6).

Arrows are shown in text-fig. 19 attached to three landmarks on the tail. The heads of the arrows show where, in space, the same landmark would be in the next diagram. The arrows therefore suggest, approximately, the direction of travel of the three landmarks in question, and the lengths of the arrows are proportionate, in any one diagram, to the velocities of the three landmarks. On the other hand, text-fig. 19 does not imply that successive diagrams are separated from each other by equal intervals of time. The proportionate lengths of arrows in different diagrams therefore mean nothing.

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TEXT-FIG. 19. *Barrandocarpus norvegicus* sp. nov. Reconstructed locomotory cycle. The arrows record the movements of three landmarks on the tail as between one figure and the next. The time intervals between figures are not supposed to be equal. The horizontal lines represent the sea bed. The vertical line is an arbitrary fixed mark. Further explanation in text.





Forces provoked in the mud or water will be opposite in direction to the arrows of movement and equal to the forces produced by this movement. The actual size, in newtons, of such forces, will depend on many factors such as the velocity, the shape of the moving part (e.g. whether a bearing surface or a cutting edge), and whether the part is moving in undisturbed mud, in mud weakened by disturbance, or in water (here assumed to produce no resistance). In other words, the provoked force can only be guessed, not measured. The forces provoked in the mud by movements of the tail will be transmitted to the rear of the head and cause the head to move—whether by translation (forwards or rearwards) or rotation (yawing, pitching, and rolling). Rotational movements are assumed to have been too small to be shown in the diagrams.

Ribs are restricted to the rear part of the head in *B. jaekeli* and similar members of the scion of *A. guttenbergensis*. This is probably for two reasons: 1, the mud in contact with the anterior part of the head will have been disturbed and weakened by the previous motion of the head and tail across it and so, perhaps, would not have been strong enough for the ribs to grip; and 2, rotational forces exerted by the tail on the rear part of the head during the return stroke (at which time the ribs would function) would be stronger than those exerted indirectly on the front part of the head.

Text-fig. 19/1 shows the beginning of the locomotory cycle, i.e. the start of the return stroke. The hind tail was moving downwards and the styloid rearwards. Resistance to this movement would be decreased by the fact that the dorsal mid-line of the hind tail was a series of knife edges, serving to cut downwards through the mud. Nevertheless, the movement of the tail would provoke an upwards and forwards force in the mud which, transmitted to the head, would tend to lift the rear of the head and push the head as a whole forwards (in the unwanted direction). This force would be resisted by the cuesta-shaped ribs, particularly of the dorsal surface of the head.

In text-figs. 19/2 to 19/12, the hind tail moved rearwards through the mud, but resistance would be reduced by the fact that the hind tail was moving mainly along its own length. The force acting on the styloid, however, would be considerable, and would be directed downwards and forwards. It would be transmitted to the head and would tend to move the rear of the head downwards and the whole of the head forwards. The movement of the styloid, as shown in text-fig. 19/3, 4, and 5, would be partly perpendicular to the length of the tail and dorsalward. Thus the transverse and longitudinal cutting edges on the dorsal surface of the styloid would cut through the mud and decrease the forward force exerted by the mud on the styloid. The shape of the styloid is therefore a compromise between two irreconcilable needs: that of exerting (*a*) the greatest possible forward force on the mud during the power stroke (text-fig. 19/20); and (*b*) the least possible force on the mud during the return stroke (text-fig. 19/2-6). At some stage between text-fig. 19/1 and 5, the force exerted on the tail, and therefore on the head, by the mud, would change in direction from forwards and upwards to forwards and downwards. As this change proceeded, the dorsal cuesta-shaped ribs would cause less resistance to forward translation, and the ventral cuesta-shaped ribs more. Forward translation of the head, in the unwanted direction, would be worst in the early stages of the return stroke (text-fig. 19/1-3), when the styloid was moving rearwards. Later in the return stroke there would have been little forward translation. For the styloid would have been moving mainly upwards, while the hind tail would have exerted little force on the mud, because it was sliding rearwards along its own length, and because of its dorsal cutting edges.

In the latest parts of the return stroke (text-fig. 19/11-13) the styloid and hind tail would, to an increasing extent, be surrounded by water, not mud, and would therefore exert almost no force on the head.

The power stroke began at text-fig. 19/14. The almost fully extended hind tail began to move forwards and downwards. As soon as the hind tail touched the mud the flattened ventral bearing surfaces of the hind-tail plates would push downwards and forwards against the mud, producing a rearward and upward force which, transmitted to the head, would translate it rearwards. As the power stroke continued, ventral bearing surfaces situated more and more proximally would push forward against the mud and, at the same time, the distal bearing surfaces of the dorsal ossicles of the hind tail would likewise push forward against the mud, particularly in the later stages of the power stroke (text-fig. 19/18-20). Finally the styloid itself, with its transversely expanded cusps,

would push forward (text-fig. 19/19–21) until the end of the power stroke at text-fig. 19/22. At this time the cycle would be ready to begin again, the head having moved considerably rearward.

To make a comparison among the forms whose locomotion was reconstructed in Jefferies (1984), the most similar to *B. norvegicus*, in most respects, is *A. guttenbergensis* Kolata and Jollie. *B. norvegicus* differs from this species, however, in some aspects of the tail morphology. In particular, the anterior cusp of the styloid is transversely elongate in *B. norvegicus* and there are well-developed bearing surfaces on the ventral plates of the hind tail in this species. The reconstruction of the locomotory cycle in *B. norvegicus* explains these differences by proposing that, at the beginning of the power stroke, the ventral bearing surfaces would push forward more effectively than in *A. guttenbergensis* and that, towards the end of the power stroke, the styloid would push forward more effectively.

Naturally, the reconstructed locomotion has a large element of guesswork, especially in its quantitative aspects such as how far the head would move rearwards in the power stroke or forwards in the return stroke. Qualitatively, however, it is likely to be right, since it explains many observed details. Those who think, with Philip (1981), that mitrates lived with the dorsal surface downwards, but none the less pulled themselves rearwards by their tails, should try to produce a reconstruction of the locomotory cycle as coherent as ours. We believe they will never succeed.

#### SYSTEMATIC POSITION

In Jefferies (1986, chapters 8, 9) it is argued that all known mitrates can be regarded as stem-group acraniates, as stem-group tunicates, or as stem-group craniates (there called stem-group vertebrates). *B. norvegicus*, along with its closest relatives, is a stem-group craniate.

The stem-group craniate mitrates can, at present, be divided into three plesions, as discussed in Jefferies (1986). In crownward order these are the plesions of: 1, *Chinianocarpus thoralis*; 2, *Mitrocystites nitra*; and 3, *Mitrocystella*. *B. norvegicus* belongs to the last and most crownward of these plesions, on the basis of many detailed resemblances with other members.

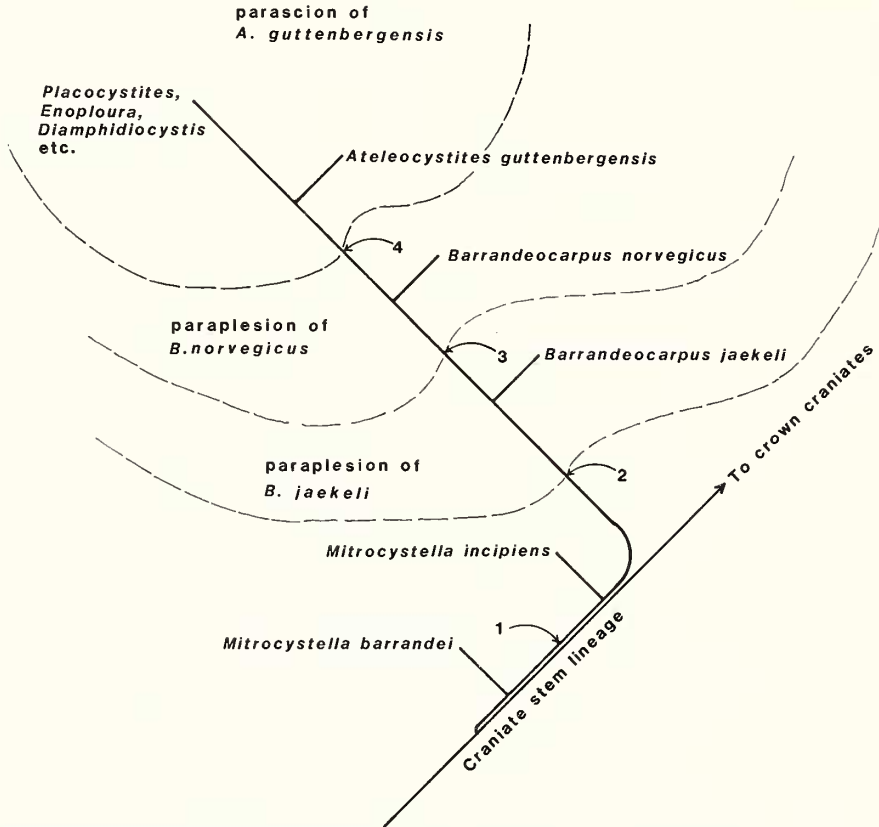
The *Mitrocystella* plesion is a diverse one comprising the following genera: *Allaicyctidium* Caster and Gill (in Ubaghs 1967); *Anomalocystites* Hall 1859; *Ateleocystites* Billings 1858; *Australocystis* Caster 1954; *Barrandecarpus* Ubaghs 1979; *Basslerocystis* Caster 1952; *Diamphidocystis* Kolata and Guensburg 1979; *Enoploua* Wetherby 1879; *Mitrocystella* Jaekel 1900; *Notocarpus* Philip 1981; *Placocystella* Rennie 1936; *Placocystites* de Koninck 1869; *Rhenocystis* Dehm 1933; *Tasuaicyctidium* Caster 1983; *Victoriaecystis* Gill and Caster 1960; *Willmanocystis* Kolata and Jollie 1982.

It would be premature to attempt a complete cladogram for these forms since many of them are inadequately known. The nodal group of the plesion is the genus *Mitrocystella* since this has not lost its lateral line and nor is it otherwise disqualified, in terms of features, from belonging to the chordate stem lineage. Both of the two described species, however—*M. barrandei* Jaekel and *M. incipiens* Barrande—are stratigraphically too late to be ancestral to crown-group craniates. For they are known respectively from the Llanvirn and the Llandeilo whereas the earliest known fossil fish, with a phosphatic skeleton, is *Anatolepis* cf. *heintzi* from the Upper Cambrian (Repetski 1978).

Within the plesion of *Mitrocystella*, however, there is a well-marked monophyletic group traditionally called the Anomalocystitida Caster 1952 and ranked by Ubaghs (1967) as a suborder. This group is characterized by a pair of oral spines articulated to the head right and left of the mouth. The spines are probably homologous with the rightmost and leftmost spike-shaped oral plates in such a form as *Mitrocystella*. As spines, they are very distinctive and probably evolved only once. The Anomalocystitida comprise all the genera listed above as belonging to the *Mitrocystella* plesion, except for the spineless genera *Mitrocystella* and *Barrandecarpus*. Within the *Mitrocystella* plesion, the first order apical group, whatever it may be, would have had oral spines (or conceivably would have secondarily lost them), and so lay somewhere within the Anomalocystitida. The latter group was therefore a first order parascion, as defined above. One



of the least apical members of this parascion is the species *A. guttenbergensis*, which has been thoroughly described by Kolata and Jollie (1982). It differs from *B. norvegicus* mainly by having oral spines. We shall therefore refer to the Anomalocystitida, henceforth, as the parascion of *A. guttenbergensis*. This follows the procedure proposed above, that a monophyletic group containing fossils, whether a scion or a parascion, should be named after its most primitive known member,



TEXT-FIG. 20. The systematic position of *Barrandeocarpus norvegicus* sp. nov. and some other members of the plesion of *Mitrocystella incipiens*. The basal part of the apical lineage of the plesion is shown adnate to the craniate-stem lineage because it may, or may not, have been part of that lineage. The arrows represent evolutionary novelties, as follows: 1, cuesta-shaped ribs appear on ventral surface, loss of plate 3 or 4 (from anterior left of head); 2, major plates of fore tail sutured to form rings, reduction in area of posterior surface of head, loss of lateral line, loss of plate 5 or 6 (from anterior right of head), cuesta-shaped ribs on dorsal surface, individualization of plate xi, reduction of number of ventral plates with individualization of ventral plates i, viii, x, vii, projection of plate p rearwards so as almost to separate g from j; 3, individualization and regularization of plates  $\alpha$ ,  $\beta$ , iv,  $\gamma$ , and  $\delta$  to form rigid anterior frame of ventral skeleton, tessellation (rather than imbrication) of all plates in anterior third of ventral skeleton so making it rigid; 4, individualization and symmetrization of ventral plates between the anterior edge of the ventral skeleton and plate xi; modification of the leftmost and rightmost oral plates to form oral spines articulated to plate (3 or 4) on the left and plate (5 or 6) on the right—the changes at 4 delimit the parascion of *Ateleocystites guttenbergensis* (Anomalocystitida) which is not further analysed here.



i.e. after the known species most closely related to the latest common stem species of the monophylum.

Within the *Mitrocystella* plesion, *B. norvegicus* represents a paraplesion less apical than the parascion of *A. guttenbergensis* but more apical than the paraplesion of *B. jaekeli*. It is more apical than *B. jaekeli* in that the most anterior ventral plates are standardized within the species and individualized as plates  $\alpha$ ,  $\beta$ , vi,  $\gamma$ ,  $\delta$ , and that the ventral skeleton immediately behind these five plates is rigid and consists of fewer plates than in *B. jaekeli*. It is less apical than *A. guttenbergensis* in lacking oral spines and in the fact that the ventral plates of the region in front of the transverse level of plate xi, but behind plates  $\alpha$ ,  $\beta$ , vi,  $\gamma$ , and  $\delta$ , are irregular and not bilaterally symmetrical. Text-fig. 20 summarizes the likely evolutionary relationships.

The *Mitrocystella* plesion is the most crownward known among the mitrate craniates—just crownward of it the skeleton was lost in the craniate stem lineage. We cannot tell therefore where the more crownward part of this stem lineage separated from the plesion. Of the two described species of *Mitrocystella*, *M. incipiens* is more closely related to the *A. guttenbergensis* parascion than is *M. barrandei*. This is shown by two synapomorphies—the presence of ventral cuesta-shaped ribs and the loss of plate 3 or 4 (it is impossible to say which) on the left side of the head. However, as already explained, the two described species of *Mitrocystella* belong to the nodal group of the plesion (i.e. they are not disqualified by their features from belonging to the craniate stem lineage) and are put in the same plesion precisely because we cannot tell which, if either, is more crownward. The synapomorphies shared by *M. incipiens* with the *A. guttenbergensis* parascion but not with *M. barrandei* could have evolved in the craniate stem lineage, or in the apical lineage of the plesion. We express this uncertainty in text-fig. 15 by making one of the segments linking the two species run parallel (adnate) to the craniate stem lineage as drawn. This signifies ignorance—we do not know whether or not these parts of the respective lineages were one and the same.

## CONCLUSIONS

This paper reconstructs and describes the first mitrate known from Norway. It is very similar to other known forms, though it undoubtedly deserves to be placed in a new species. It is a stem-group craniate and thus contributes to our knowledge of the earliest evolution of a group to which we ourselves belong.

Its placement in cladistic terms, within the plesion of *Mitrocystella*, requires discussion of the plesion concept and an attempt to refine how fossils can be systematized within a plesion. Using the concepts discussed above under 'Phylogenetic methodology', we treat the group traditionally called the Anomalocystitida as a first order parascion within the plesion of *Mitrocystella* and we refer to it as the parascion of *A. guttenbergensis*, after its most primitive well-described member. *B. norvegicus* represents a paraplesion less apical than this parascion, but more apical than the paraplesion of *B. jaekeli*. The least apical paraplesion within the plesion of *Mitrocystella* is that of *Mitrocystella* itself. This represents the nodal group of the plesion.

We believe that, unlike recent organisms, fossils require paraphyletic groups for their complete systematization. Consideration of *B. norvegicus* helps to answer the basic question of how these groups can be made objective.

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A. J. CRASKE  
 18 Fairview Road  
 Chigwell, Essex IG7 6HN

R. P. S. JEFFERIES  
 Department of Palaeontology  
 British Museum (Natural History)  
 London SW7 5BD

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